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THE PROBABLE FUTURE DISTRIBUTION OF THE JAPANESE BEETLE IN NORTH AMERICA

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INTRODUCTION

The Japanese beetle, *Popillia japonica* Newman, is now known to be present in this country at numerous localities extending from

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[1] The studies upon which this paper is based were begun unofficially early in the period of employment of the writer as Associate Entomologist, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture. It was only for a relatively short period toward the end of his connection with the Bureau that the subject was specifically recognized as an official project of investigation. Following the writer's detachment from the Bureau the same line of studies was continued independently at New York University and the results to date are here presented as a contribution from the Department of Biology of that institution.

Some of the conclusions reached in this study were published in advance by C. H. Hadley (Jour. N. Y. Ent. Soc. XLVI: 203–216, 1938). One paragraph in his article on the ultimate distribution of the beetle (p. 203–204) is an almost verbatim transcript of a summary furnished Mr. Hadley at his request. In the article as published, customary acknowledgment of the source of the information was withheld.

Editor's Note: Under date of December 1, 1938, I was advised by Dr. Lee A. Strong, Chief of the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture, that Mr. Hadley's manuscript was submitted to the Bureau for approval on December 12, 1935, and that it included a reference to an unpublished "report" by Doctor Fox, which summarized studies carried on by him up to that time as an employee of the Bureau, as well as references to other unpublished reports. In accordance with the general practice of the Editorial Office of the Bureau, these citations were deleted.

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south-central Maine and north-central New York south to northern South Carolina and west as far as Detroit, Michigan, Chicago, Illinois, and St. Louis, Missouri. Since the insect has maintained itself for the past five or six years in such outlying points of its apparent range as Brewer, Maine, Greenville, South Carolina, and St. Louis, Missouri, its establishment is likely to be permanent in most, if not all, the localities from which it has been hitherto reported, unless checked by artificial means. Although in the vastly greater part of the area, whose limits are approximately defined by the localities cited, the Japanese beetle occurs only in the form of local colonies more or less widely separated from one another and from the present main distribution area of the species in New Jersey and neighboring states, there can exist little doubt that eventually the intervening country will be occupied as a result of the meeting and coalescence of the various local areas of dispersal originating in and progressively expanding about these centers.

The apparently permanent establishment of the beetle at numerous points distributed throughout an area embracing the greater part of the eastern third of the United States obviously points to the existence within that section of environmental conditions to which it is generally adapted. This view is in accord with the known reactions of the Japanese beetle to temperature and humidity and is also substantiated by a comparison of the climate of this country with that of Japan, which shows that the latter is most nearly duplicated in those parts of the United States where the Japanese beetle is now present.

In insects which, like the Japanese beetle, pass the greater part of their annual life-cycle beneath the surface, the more obvious environmental factors conditioning their distribution are, apart from oceanic barriers, temperature and precipitation. While these as generally recorded are atmospheric phenomena, they produce effects underground which are closely correlated with the changes occurring above the surface.

TEMPERATURE RELATIONS OF THE BEETLE

The studies of Ludwig (1928, A) have shown that the effective range of temperature for development in the Japanese beetle extends from about 12° C. (53.6° F.) to 35° C. (95.0° F.). However, the insect appears to be capable of passing through the complete life-cycle only at temperatures ranging between 17.5° C. (63.5° F.) and 27.5° C. (81.5° F.). The reason is that a temperature which may be suitable for certain developmental processes may be prohibitive to others essential to carry the insect through the complete life-cycle.[2]

The temperature of the air necessarily influences that of the ground, especially near the surface where the daily fluctuations conform to the same general pattern, except for a marked decrease in total range due to the lag in change of temperature arising from the poor conductivity of the soil. Where the plant cover does not preclude penetration of the direct rays of the sun, part of the rise of temperature in the immediately underlying layers of the soil results from their absorption. Hence, throughout most of the season of Japanese beetle activity and reproduction the daily rise of temperature in the soil at the shallow depths occupied by the insect more nearly approaches that attained in the air than does the fall of temperature during the night. During this period the temperature of the soil in such situations thus averages from one to several degrees higher than that of the air as computed from the readings of the ordinary air-exposed thermometer. Accordingly, when the usually recorded seasonal mean temperature of a given station is taken as an index of its suitability for Japanese beetle growth and development, it needs to be kept in mind that the mean temperature to which the insect is exposed is likely to be a degree or two higher than the recorded temperature. This is shown by records kept for the past 10 years at Moorestown, N. J., where a mean temperature in mid-summer of approximately 74.5° F. is correlated with a mean of about 77.0° F. (25° C.) at a depth of one inch in ground covered with sod, as in the usual habitat of the Japanese beetle larva.

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[2] The present writer has found that eggs of the Japanese beetle kept at a constant temperature of 54° F. (12.2° C.) undergo some development, but fail to hatch. However, other eggs which had passed through the greater part of their development at higher temperatures (approximately 75° F.) readily hatched when placed at 54° F. But the larvae hatched at this temperature invariably died within a few days unless transferred to a higher temperature, probably because at 54° F. the larvæ are too sluggish to feed. At the opposite extreme, Ludwig found that when the larvæ are reared throughout at a temperature of 27.5° C. (81.5° F.) only a few reached the adult stage, the others for the most part dying during the period of metamorphosis of the larva into the pupa, a result which the present writer has confirmed. On the other hand, larvæ which had passed through part of their larval development under outdoor conditions, at temperatures averaging between 65° and 75° F., completed the remainder of their development and passed through the metamorphosis without evident difficulty when kept at a nearly constant temperature of 27.5° C. (Fox, Ms.)

INFLUENCE OF SOIL MOISTURE ON SUMMER SURVIVAL

Atmospheric precipitation naturally conditions the moisture content of the soil where the greater part of the life-cycle of the Japanese beetle is passed. The dependence of the insect upon such moisture is evidenced by the annual fluctuations in its abundance as observed in its main distribution area in this country. Greatly reduced populations have been invariably correlated with a marked deficiency in rainfall during the preceding summer. The normal rainfall for the entire summer in the area in question amounts roughly to 12 inches, which, while somewhat less than in the corresponding temperature zone of Japan, appears to be sufficient to meet the moisture requirements of all stages of the Japanese beetle present at the time. However, during the period covered by the writer's observations on beetle abundance, there occurred two summers (1929, 1932) in which the rainfall in the vicinity of Philadelphia was markedly deficient, falling from 4 to 6 inches below the normal. In each case this deficiency in rainfall during the summer was followed by a Japanese beetle population much reduced below that represented in other years when more nearly normal rainfall conditions prevailed during the summers.

The reason for such striking reductions in Japanese beetle populations in connection with summer drought is doubtless to be found in the fact that summer is the season of maximum egg deposition and hatching for the insect. It is during these initial stages in its annual life-cycle that moisture, in a readily available form, is most urgently needed and its absence or scarcity most likely to prove fatal. The egg, like that of other scarabæid beetles, must absorb moisture to bring about the swelling which is the essential prelude to embryonic development, while the newly hatched larva needs it to retard desiccation until it succeeds in finding some source of food succulent enough to supply it with the needed moisture as well. Ludwig (1936), who has studied the desiccation of the Japanese beetle, states that the larva in each of its three instars can withstand a loss of body moisture equal to half its initial body weight. Further loss is fatal. In freshly hatched larvæ the actual amount of moisture lost before the fatal limit is reached would evidently be much less than in older larvæ, and hence the time required to effect desiccation correspondingly shortened. In such larvæ the surface in only very lightly chitinized and hence conserves body moisture much less effectively than in later stages when it is more heavily chitinized. Moreover the freshly hatched larva, on account of its minute size and the soft consistency of its body, can burrow only very slowly through the soil in its search for food. For these various reasons, it would seem obvious that any marked lack of moisture in the immediate surroundings would prove far more detrimental to the insect during the period of egg development and hatching than at any other period during its annual life-cycle.

Since both the egg and larva of the Japanese beetle occur in the ground, the moisture which more directly affects them is that of the surrounding soil. This is primarily conditioned by the amount and distribution of the rainfall, but is also influenced by other factors, such as the topographic situation and the texture and composition of the soil. On this account the Japanese beetle is often enabled to survive in considerable numbers in circumscribed areas where, because of sluggish drainage, moisture in the soil is retained much longer during a prolonged drought than in other parts of the affected area.

INFLUENCE OF PRECIPITATION ON WINTER SURVIVAL

Atmospheric precipitation indirectly affects the temperature of the soil. In moist ground the change in temperature in response to fluctuations in atmospheric temperature is slower than in dryer soils. Hence in a humid region sudden or extreme changes in the temperature of the air produce relatively slight changes beneath the surface, where the temperature tends to fluctuate only a relatively few degrees on either side of the seasonal mean. But the most important effect of precipitation on the temperature of the soil from the point of view of insect survival is to be found in winter, when, as Mail (1930) has demonstrated, the blanket of snow serves to keep the temperature of the subjacent soil within a few degrees of the freezing point (0° C.; 32° F.), even during prolonged periods of intense cold, which otherwise would prove fatal to the insects present in the ground.

In connection with this latter effect, the capacity of the Japanese beetle larva to withstand cold is important, the larva being the stage in which the insect passes the winter. Data from several sources, including some recent unpublished observations by the writer, point to +15° F. (−9.4° C.) as the lowest temperature which the larva could withstand under natural conditions. Air temperatures in winter, in most of the areas at present occupied by the Japanese beetle, frequently range far below this lethal point and the fact that notwithstanding the insect has survived in undiminished strength is attributable to the protective covering of snow which kept the temperature of its subterranean habitat well within the limits of cold tolerance of the larva.[3]

TYPE OF COUNTRY FAVORABLE FOR THE BEETLE

The foregoing facts indicate the adaptation of the Japanese beetle to a country having (1) a range of temperature capable in the summer of maintaining the mean temperature of the soil within limits (17.5°–27.5° C.) favorable for the hatching of the eggs and the survival of the early larvæ, and (2) a precipitation copious in amount and rather uniformly distributed throughout the year, thereby in summer furnishing the soil moisture needed to prevent desiccation of the eggs and freshly hatched larvæ, and in winter providing the protective covering of snow serving to keep the temperature of the ground within the limits of cold tolerance of the larvæ.

CLIMATE AS A POSSIBLE LIMITING FACTOR IN JAPAN

These conditions are admirably fulfilled in the original home of the beetle in Japan, where its range, with the possible exception of a narrow belt along the extreme northern and northeastern coast of the northernmost island, Hokkaido, appears to be coextensive with the entire archipelago of four large islands which constitute Japan in the usual restricted meaning of the term.[4] Within these limits, the mean temperature of the summer is reported as ranging from 13.6° C. (56.5° F.) at the extreme eastern tip of Hokkaido (Nemuro) to 25.0° C. (77.0° F.) near the southern extremity of the country (Kagoshima). But within the portion in which the beetle is definitely known to occur, the lowest mean reported for the summer is 17.1° C. (62.6° F.). If means lower than the latter be disregarded, the range of summer temperatures in Japan points to the general prevalence in the soil (sod land) of that country of summer means falling within the postulated limits (17.5°–27.5° C.) for normal development of the beetle. As regards precipitation, Japan is reputed one of the wettest countries in the world, the rainfall often being extremely heavy and usually well distributed throughout the year. In winter snowfall is stated to be scanty in the southern half of the country, but very heavy in the extreme north where it presumably enables the beetle to survive such severe winters as prevail in the interior of Hokkaido (Asahigawa) where a temperature as low as –41° C. (–41.8° F.) has been reported.

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[3] At Moorestown, N. J., during the excessively cold winter of 1934 at the same time that the minimum for the season of −13° F. was recorded, the temperature in the soil at a depth of only 1 inch below the surface was +27° F., within 5 degrees of the freezing point.

If the Japanese beetle is indeed absent in that section of Hokkaido, as about Nemuro and elsewhere along the northeast coast of that island, from which there are no definite records of its occurrence, it follows that, if climate is alone involved, the limiting factor in its northward range in Japan is the low temperature of the summer rather than the cold of winter. The beetle is reported as common and generally distributed in the interior of Hokkaido where the winters are most severe, while it is absent or scarce in a section where, because of the low altitude and the proximity of the ocean, the temperature in winter is considerably milder, but where in summer it averages lower than in any other part of Japan.

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[4] For detailed data on the occurrence of the beetle in Japan the writer is indebted to J. L. King, T. R. Gardner, and L. B. Parker. Their scouting records indicate its general prevalence throughout the three southern islands and in most of Hokkaido, but leave unsettled its status in the more outlying northern and northeastern sections of the latter, where their scouting, as at Nemuro and other nearby localities yielded only negative results. It is possible that the absence, or at least marked scarcity, of the insect in this section of Hokkaido may be due to the fact that it is only in this highly restricted part of Japan that the temperature during the summer averages below the lowest limit (17.5° C.) favorable for the development of the eggs and early larvæ. However, as Gardner has suggested to the writer, it may be that the heavily forested state of the country adjoining Nemuro and other nearby towns is also responsible for the local scarcity of the beetle.

How effective high temperatures are likely to prove in limiting the southward range of the Japanese beetle is a problem upon which a knowledge of its distribution in its native country sheds no light, the obvious barrier to its spread in that direction being the ocean rather than any climatic condition. In experiments no beetles have been reared through the complete life-cycle when constantly exposed to a temperature above 27.5° C., but in nature constant temperatures are highly exceptional and Japanese beetles reared under variable temperatures have been found to withstand exposure to higher temperatures more successfully than those retained throughout their life at such temperatures.[5]

SECTION OF NORTH AMERICA FAVORABLE TO THE BEETLE

Since a country with the climatic features of Japan is indicated by the evidence at hand as preeminently suitable for the Japanese beetle, it is likely that the insect will find conditions most favorable to its permanent establishment in those parts of this continent where the climate in its totality most nearly duplicates that of Japan. In a general sense, this is the case in all that portion of the United States and southern Canada which lies east of the 100th Meridian; in other words, in what is known as the Humid Belt of North America. It is in this portion of the continent that, along with an annual range of temperature similar in general to that of Japan, precipitation is normally both copious in amount and rather generally and uniformly distributed throughout the year. Farther west the country is either too dry at all times, or else during certain critical periods in the year, to offer any general climatic conditions comparable with those of Japan.

RAINFALL AS THE MAJOR LIMITING FACTOR IN THIS COUNTRY

The probability that rainfall will prove a potent factor in limiting the future range of the Japanese beetle in this country is in a measure substantiated by the fact earlier mentioned that greatly reduced populations of the insect have been invariably observed following summers with a marked deficiency in rainfall. In general, it would seem that a total rainfall for the summer of less than 10 inches is likely to prove detrimental to the species. It, therefore, seems safe to infer that it would find conditions strongly adverse to its permanent establishment in those portions of this country where, as in the western interior, an arid or semi-arid climate is the rule, or where, as on the Pacific Coast, the summers are generally rainless.[6]

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[5] See footnote 2.

Although the entire eastern half, or Humid Belt, of the United States exhibits climatic conditions in fairly close agreement with those of Japan, it deviates from the latter in several ways, notably in its more variable rainfall. In Japan the rainfall appears to be almost invariably copious at all times during the year, with relatively little variation in its quantity from year to year. Droughts, except in very restricted areas, are said to be practically unknown. In the United States, on the other hand, droughts at irregular, though rather frequent, intervals form a characteristic feature of the climate, even in its normally well-watered eastern sections. Hence, the probability of the occurrence of protracted droughts during the summers, with their more or less detrimental effects upon Japanese beetle populations, is considerably greater in this country than in the original home of the beetle in Japan. Such droughts naturally tend to increase in frequency and severity in sections where the rainfall is normally lighter, as in parts of the central Mississippi valley, where the rainfall in summer averages from two to four inches less than in the states adjoining the North Atlantic coast. It accordingly seems probable that the Japanese beetle will find rainfall conditions in the central Mississippi basin and other east-central sections of this country somewhat less favorable than in its present main distribution area near the eastern seaboard.

Despite the potential danger to Japanese beetle survival arising from the relative frequency of protracted droughts during the summers, it is questionable if there is any part of the eastern half of this country in which elimination of the insect from this source would be more than transitory. Observations in the Philadelphia area have shown a marked predilection of the beetle during dry seasons to select low-lying, sluggishly drained tracts in which to deposit its eggs. In such situations, owing to the proximity of the water-table to the surface and seepage from the surrounding higher ground, the soil is likely to retain a moisture content favorable to the insect for a much longer period than elsewhere in the vicinity. This habit obviously favors its survival in a drought-stricken district. Such observations suggest that to effect a reduction in the numbers of the beetle to the point of extermination a drought would have to be sufficiently prolonged to bring about a cessation of flow in all except the major streams of a district. While this has happened repeatedly in various parts of the eastern half of the United States, it is only very rarely that droughts of such severity extend simultaneously over more than a limited area. Hence, even if in a given area a drought would effect the elimination of the insect, it would not be long before it would be again populated because of the survival of the beetle in some adjoining area where the rainfall was more nearly normal.[7] Hence the chance of droughts serving to eliminate the Japanese beetle throughout any considerable part of the eastern half of the United States would seem to be very slight. About all that can be expected is that the greater frequence of prolonged summer droughts in much of the central Mississippi basin would tend to keep its Japanese beetle populations reduced to more moderate numbers than in the more humid sections of the country bordering the Atlantic coast.

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[6] This remark would not necessarily apply in local instances where, as a result of artificial irrigation, conditions typical of the region have been radically altered.

WINTER CLIMATE AS A POSSIBLE LIMITING FACTOR IN THE NORTHWARD SPREAD OF THE BEETLE

Although it is highly questionable whether droughts in summer are likely to have more than a local, or at most moderately reducing, effect upon Japanese beetle abundance throughout the normally well-watered eastern half of this country, there exists one section in which there is reason to believe that the normally light precipitation in winter may interact with the temperature to produce a condition prohibitive to the permanent survival of the insect. This is the region lying west of, and in the same general latitude as, the Great Lakes and extending thence to the Missouri River. In this section, which is usually termed the Northern Interior, occur the most severe winters within the limits of the continental United States. It comprises the entire state of Minnesota along with much of Wisconsin and of North and South Dakota and the northern half of Iowa. Within the limits thus roughly defined, the temperatures normal to the winter fall definitely below the lowest normals for the same season recorded from Japan, although the differences in absolute minima (−43° F. and −42° F.) are not impressive.

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[7] A perusal of the detailed data on precipitation published in the Climatic Summary of the United States by Sections shows that in practically all of the country lying east of the 100th Meridian summer droughts of exceptional severity practically never extend simultaneously over more than a limited area. Even a drought as widespread as that of the summer of 1930, although rather general over most of the East, was far from being universal, the continuity of the several drought areas being more or less extensively interrupted by belts of more nearly normal precipitation intercalated between them.

The relatively light winter precipitation of this section, averaging less than 4 inches, increases the chance of a prolonged period of sub-freezing temperature coinciding with an absence of snow. The larva of the Japanese beetle can be killed by lowering the temperature of the ground, at the depths occupied by it in winter, to the lethal point, which as earlier stated, appears to be approximately +15° F. As Mail (1930) has shown, it is only when snow is absent that intense cold is capable of lowering the temperature of the soil more than a few degrees below the freezing point. This condition was actually realized in the course of the particular winter during which Mail's observations were made at Minneapolis. A mid-winter thaw, resulting from a ''warm wave,'' caused whatever snow had been present to vanish and this was succeeded by a ''cold wave,'' with daily temperatures for nearly a month almost uninterruptedly averaging below +20° F. As a result, refrigeration of the soil progressed until a temperature of +15° F. was reached at all depths as far down as a foot below the surface. Since in their usual habitats Japanese beetle larvæ do not winter at greater depths, it follows that a similar refrigeration of the soil in a place where they chanced to be present would result in their practical, if not complete, extermination.

A winter climate comparable in severity with that of the Minneapolis district and characterized by an equally light precipitation prevails generally as far south as southwestern Wisconsin, central Iowa and northeastern Nebraska. If present views as to the cold tolerance of Japanese beetle larvæ are sound, and if a similarity of general climatic conditions may be taken as an index of the occasional coincidence of the low temperatures normal to the region with a general absence of snow, it would seem that in the northern interior of this country any permanent extension of range of the Japanese beetle north of the latitude of central Iowa is precluded.

In the region of the Great Lakes and thence east to the Atlantic Ocean the precipitation in winter is normally so copious as to make highly improbable the coincidence of a prolonged period of intense cold with the absence of a snow cover. Furthermore, in correlation with the increased humidity which is thus implied, the temperature in winter of this more eastern section of the country averages considerably higher than in the northern interior, making all the more improbable the occurrence within its limits of any combination of circumstances likely to seriously militate against the spread of the Japanese beetle throughout New England, New York and the Lower Peninsula of Michigan, as well as across the border into the adjoining provinces of Canada.

SUMMER TEMPERATURE AS A LIMITING FACTOR IN THE NORTHWARD SPREAD OF THE BEETLE IN THE EAST

In all parts of this country where precipitation throughout the year is normally copious, the effective barrier to the northward spread of the Japanese beetle is less likely to be the severity of the winters than the low temperatures of the summers, which in the more northern portions would either inhibit the hatching of the eggs or prevent the survival of the young larvæ. Within the United States the northward limits of spread of the beetle in the East will probably fall near Eastport, Maine, with a temperature in summer almost identical with that of Nemuro, Japan, in the more elevated sections of northern New England and New York, and in extreme northern Michigan. Elsewhere the beetle is likely to extend its range across the border into the adjoining sections of Canada, as far along the St. Lawrence as Montreal at least and in the interior to Georgian Bay.[8]

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[8] According to data obtained by Ludwig, eggs of the Japanese beetle kept at a constant temperature of 17.5° C. (63.5° F.) take from 31 to 37 days to

SUMMER TEMPERATURE AS A LIMITING FACTOR TO THE ESTABLISHMENT OF THE BEETLE IN THE WEST

Rainfall in summer on the crests of the higher mountain ranges of the West, as the Rockies and the Cascades, would doubtless be sufficient to furnish the soil moisture needed by the Japanese beetle in its early stages, but the low temperatures of the summers at such altitudes would probably preclude its establishment. Along the Sierra Nevada the moisture stored in the ground from the melting of the heavy snowfall of the winters would favor the beetle, but, as in the other cases mentioned, the cold summers would probably be prohibitive to its survival.

Essentially similar conditions would presumably make difficult the establishment of the beetle along the more northern sections of the Pacific Coast, as in Oregon, Washington and Vancouver, where the rainfall in summer, while generally scanty, is heavier than farther south.

THE PROBLEM OF THE FUTURE SOUTHWARD SPREAD OF THE BEETLE IN THE EAST

It has already been stated that one section exists within the eastern half of the United States where the temperature in winter normally averages lower than the lowest winter mean recorded in Japan. This is the northern interior, in which conditions have been indicated as probably inimical to the Japanese beetle. At the opposite extreme, a section also exists, embracing much of the South Atlantic and Gulf States, in which the temperature during the summer averages higher than the highest mean recorded in

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hatch, while at 15° C. (59° F.) they take from 53 to 67 days. The average mid-summer temperature of Eastport is approximately 16° C. (60.8° F.). The low temperatures of the late spring (50°–52° F.) and early summer (52°–60° F.) at that locality would retard development of the insect, so that adult emergence could scarcely occur and egg deposition begin before August 1. In consequence hatching would not start at the earliest before September 1, and with the rapidly falling temperatures of that month (mean 55.8° F.) it seems unlikely that the resulting larvæ would consume sufficient food before cold dormancy sets in to enable them to survive. Ludwig (1928, B) has shown that while recently hatched larvæ which have fed for some time prior to hibernation are capable of surviving the winter, those which have not fed soon perish if exposed to a temperature no lower than 10° C. (50° F.).

Japan. In this country the isotherm of 25° C., the highest summer mean of Japan, coincides very nearly with the northern limits of the Cotton Belt, as mapped in the publications of the Department of Agriculture (*e.g.,* Agelasto *et al.,* 1921). It is noteworthy that up to the present no instances are certainly known of the permanent establishment of the Japanese beetle south of this isotherm.[9] However, no facts are definitely known which would preclude the eventual extension of the insect's range across the intervening country to Florida and the Gulf Coast. In Japan, as previously noted, the ocean, rather than any extremes of temperature, forms the obvious barrier to any further spread of its range south of its present limits in that country. In the United States, in the absence of a definite geographic barrier, no apparent obstacles exist to prevent the southward spread of the beetle. Evidently the southward limitation of its range in Japan to a district with a summer mean of 25° C. (77° F.) can scarcely be accepted as a valid criterion of any incapacity on its part to occupy all that portion of the eastern half of this country which has a summer mean in excess of 25° C.

Although it cannot be definitely asserted that any clearly demonstrated barrier exists to the future spread of the Japanese beetle throughout the South Atlantic and Gulf States,[10] certain features of the life-cycle of the beetle suggest that the high temperatures, and consequently prolonged season of insect activity, in that section may prove less favorable to it than might be expected. High temperatures, if not extreme, accelerate development. Although, on the basis of results reported by Ludwig (1928, A), it cannot be premised that the rate of development of the Japanese beetle is controlled by temperature alone, nevertheless the bare possibility exists that, under temperature conditions like those of the Southern States, the insect, by the time winter sets in, will have reached a stage in its life-cycle at which it appears to be highly sensitive to even moderate cold. This is the stage known as the prepupa when the larva is in process of transforming into the pupa. Such prepupæ reared experimentally have been found to perish in large numbers when chilled for a day or two at a temperature no more extreme than 40° F. If temperatures in the South remain sufficiently high during the season of active growth to bring a large proportion of the larvæ to this critical stage before the arrival of winter, it is at least possible that the subsequent chilling to which they would be subjected would result in a high mortality. Such mortality, if it occurred, would tend to keep the Japanese beetle populations of the region greatly reduced compared with those represented in more northern latitudes and, as a result, to retard their further spread.

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[9] Scattered occurrences of the beetle have been reported south of this isotherm as far as Charleston, S. C., and, according to more recent information furnished by J. L. King, to Atlanta and Savannah, Ga. However, the small numbers taken in most of the localities, as well as the fact that all except a few of the occurrences are situated close to the isotherm in question, leaves problematical the permanent establishment of the species at any point located well within the Cotton Belt.

[10] Excepting those parts of Texas which have an average summer rainfall of less than 10 inches.

The question of the possible establishment of the beetle in tropical and subtropical Florida merits special consideration. Even though it may be unable to cross the Cotton Belt, there remains the probability of its introduction into that section of the state through artificial conveyance. Since experiment has clearly shown that the Japanese beetle is capable of passing through its complete life-cycle at temperatures between 17.5° and 27.5° C. (63.5° and 81.5° F.), the temperature of southern Florida would offer no obstacle to its establishment. At all times of the year, as at Tampa, for example, the average temperature falls well within the limits of safety for the species, in winter rarely falling below 50° F. and in summer seldom averaging above 81.5° F., while the rainfall is copious, especially during the warmer half of the year. Under such conditions the beetle would be able not only to survive but would probably be two-brooded, since two generations a year have been obtained experimentally when reared at 25° C.

There remains, of course, the chance that factors other than climate might interpose a barrier to the permanent establishment of the species. Much of the soil of southern Florida is sandy and rather porous and it has been found that in those sections of New Jersey where such soils predominate the beetle has remained decidedly scarce as compared with its numbers in the sections having the finer and more loamy soils. Moreover, the native vegetation of southern Florida is largely composed of dry and coarse types of plants and the land as a whole appears unsuited for the support of such tender and succulent grasses as form the bulk of the plant cover in the usual haunts of the insect in the North. However, the recent transformation of extensive sections of southern Florida into country estates and farm lands has radically changed the original conditions and doubtless made the country more favorable for colonization by the beetle.

The foregoing remarks would doubtless apply to all sections of tropical or subtropical America where the rainfall is copious and the soil and vegetation suited to the beetle.

SUMMARY

The known reactions of all stages of the Japanese beetle to different degrees of temperature and humidity indicate its adaptation to countries with (1) a range of temperature capable of keeping the mean summer temperature of the soil occupied by the insect within the limits (17.5° C. and 27.5° C.) favorable for the hatching of the eggs and the survival of the larvæ, and (2) a precipitation copious in amount and rather uniformly distributed throughout the year.

The temperature of the soil in the type of ground inhabited by the Japanese beetle throughout most of its life-cycle is indicated as averaging slightly higher than that of the air during the season of growth and development. This fact needs to be considered when the seasonal mean temperature of a locality is taken as an index of its suitability for the permanent establishment of the beetle.

Precipitation is indicated as influencing survival through its effects on the moisture content of the soil, especially during the season of egg deposition and hatching. Greatly reduced beetle populations in the area in this country where the beetle is normally abundant have been correlated with summers of deficient rainfall.

Precipitation in winter influences survival by providing the covering of snow, which in regions with air temperatures fatal to the species serves to keep the temperature of the subjacent soil well within the limits of cold tolerance of the larvæ. 15° F. is indicated as the lethal point under natural conditions.

In Japan the low temperature of the summers near the northern limits of its range is probably the limiting factor in determining the spread of the beetle in that direction rather than the cold of the winters. At its southern extremity further spread is barred by the ocean. For this reason the climatic conditions coincident with the southern limits of the beetle's range in its native land cannot be utilized as a valid criterion of any incapacity on its part to establish itself in countries with a warmer climate than Japan.

In this country it seems highly probable that the Japanese beetle will eventually spread throughout and become permanently established wherever the normal conditions of temperature and precipitation most nearly resemble those of Japan. The region so characterized lies east of the 100th Meridian and, in general, extends from the lower Canadian provinces south to the upper limits of the Cotton Belt, formed by the summer isotherm of 77° F. (25° C.). Within these limits the beetle is likely to find conditions most congenial in the section bordering the Atlantic, but it will also find them nearly as favorable in the interior, as in the Mississippi valley, where, however, the greater frequency of prolonged droughts in the summers will probably tend to keep it less abundant than east of the Appalachians.

Rainfall, especially in summer, is indicated as the major limiting factor in determining the future range of the Japanese beetle in North America. It is apparently not adapted to an arid or semiarid climate and hence is not likely to become generally established in the western half of this continent.

In that section of this country which extends from the Great Lakes east to the Atlantic, where the precipitation is normally copious throughout the year, the effective barrier to the northward spread of the beetle will doubtless be the low temperature of the summer rather than the severity of the winters.

In the region lying west of and in the same general latitude as the Great Lakes and extending thence west to the Missouri River, where the precipitation in winter is normally light, the extreme cold of the winters in combination with a wide-spread absence of snow is likely to be the limiting factor in stopping the northward advance of the beetle.

In those limited portions of the West where precipitation, or the accumulated moisture in the ground, would favor the establishment of the beetle, as on the crest of the higher mountain ranges and the more northern sections of the Pacific coast, the low temperature of the summers would doubtless prove effective in preventing it.

In the eastern half of this country no geographic barrier exists to hinder the eventual southward spread of the beetle across the Cotton Belt to Florida and the Gulf Coast, although the possibility is indicated that its spread south of the summer isotherm of 25° C. (77° F.) may prove difficult owing to the shortening of the life-cycle resulting from the high temperature and long duration of the growing season. This suggests the possible appearance late in the season of stages likely to succumb to even the moderate cold of a southern winter.

The climate of southern Florida, and of practically all sections of tropical or sub-tropical America in which rainfall is copious, is indicated as highly favorable to the Japanese beetle on the basis of experimental results. The possibility exists, however, that factors of a non-climatic nature, such as the character of the soil or the composition of the vegetation, may serve as barriers to its establishment despite the favorable climate.

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